Seasonal Patterns of Female *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) Reproductive Physiology in Riverside, California

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ABSTRACT Female *Homalodisca coagulata* (Say) were collected from October 2001 to February 2005 from citrus at the University of California, Riverside. Between 5 and 20 females per sampling date were dissected, and each was assigned an ovarian rank: previtellogenic, vitellogenic, or postvitellogenic. Ovarian ranking was used to characterize *H. coagulata* reproductive activity. Results of these dissections revealed consistent annual patterns in the proportion of previtellogenic females present in this field population. These patterns indicate that there are two distinct generations annually, with an occasional third generation. A time-dependent model of *H. coagulata* vitellogenesis cycles in Riverside, CA, was developed, which makes it possible to predict the appearance of the subsequent generation based on previous observed peaks in the proportion of vitellogenic females.

KEY WORDS citrus, diapause, glassy-winged sharpshooter, leafhopper, telotrophic

The glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Cicadellidae: Proconiini), is a serious pest of many tree and vine crops, and a primary vector of the bacterium *Xylella fastidiosa* (Turner 1949, Wells et al. 1987), which infects many hosts (Hewitt et al. 1946, Davis et al. 1980) including grape (Alderz and Hopkins 1979), almond, and oleander (Costa et al. 2000). *H. coagulata* was first detected in southern California in 1989 (Sorenson and Gill 1996) and represents a significant threat to the California grape industry (Purcell 1999, Purcell and Saunders 1999). Adults can vector *X. fastidosa* throughout their entire life, whereas nymphs must reacquire *X. fastidosa* from an infected host after each molt (Almeida and Purcell 2003). *H. coagulata* is distributed throughout the southern United States, South America (Young 1958, Turner and Pollard 1959), and on the islands of Hawaii and Tahiti (Hoddle 2004). It is reported to have two generations per year in Florida (Alderz 1980) and in southern California (Blua et al. 1999). A third generation was reported to occur on occasion in Texas (Sanderson 1905) and Georgia (Turner and Pollard 1959).

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Estimates of number of generations per year and their timing can vary depending on the sampling method (Blua et al. 2002) and the method used to determine ages of collected nymphs and adults. Red-winged adults are considered to be young males and females (B.R. Bextine, personal communication). The brilliance of red wing color typically fades with age and may vary seasonally. Our dissection data indicate that, as a general rule, previtellogenic females have bright red and black wings, whereas vitellogenic females have faded red wings, and postvitellogenic females have orange to brown wings. However, previtellogenic females with brown wings are occasionally collected in the winter months, and these may be in a reproductive diapause (N.A.H., unpublished data).

Hix (2001) assessed the females' reproductive activity of field populations of *H. coagulata* by monitoring for the presence of "white spots" on their forewings. The white spots consist of brochosomes produced by specialized cells in the Malpighian tubules and excreted from the anus (Rakitov 1999, 2002). Vitellogenic females apply brochosome droplets to hair patches on the forewings just before oviposition (Hix 2001, Rakitov 2002). However, this assessment method is not reliable because females with these white spots do not always carry mature eggs, the white spots may be lost after they are deposited, or females may be collected before brochosomes are applied on the forewings (Hix 2001).

Homalodisca coagulata generations may overlap considerably throughout the year, making it difficult to monitor population demographics and determine

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Table 1. Criteria used to merge ovarian ranks of field-collected specimens of *H. coagulata* into categories of previtellogenic, vitellogenic, and postvitellogenic

Vitellogenic status	Ranks combined	Egg length[a]	Corpus luteum	N[b]	Notes on ovarioles
Previtellogenic	0, 1 and 2	Small to medium	Absent	261	Corpora lutea absent
Vitellogenic	3, 4, and 5	Large	Sometimes present	356	Contains one mature or maturing oöcyte
Postvitellogenic	6 and 7	Small to medium	Present	376	Corpora lutea present

[a] Length of the largest egg in each ovariole.
[b] $n_{total} = 993$.

synchrony of ovipositional events based solely on external characteristics, such as red wing color or the presence of brochosome spots on the forewings (Hix 2001). Detinova (1967) argues that the most accurate method of population studies involves determination of the physiological age of the females, based on ovary development. In this study, we determined the demographics and reproductive patterns of *H. coagulata* populations on citrus in Riverside, CA, by assigning ovarian ranks to field-collected females according to the methods of Hummel et al. (2006). Seasonal patterns of female fecundity are critical to improve timing of chemical and biological controls for *H. coagulata.*

Materials and Methods

Collection and Preparation of Insect Specimens. *Homalodisca coagulata* were collected weekly or biweekly from October 2001 to February 2005 from mixed citrus varieties in a citrus varietal collection at the Agricultural Operations (UCR Ag Ops), the University of California, Riverside. The number and composition of citrus trees varied on different collection dates, depending on the population density of adult *H. coagulata* present, but generally, we collected individuals from grapefruit, lemon, orange, trifoliate orange root stock, and unnamed citrus variety host trees over an approximate 2-ha area. Specimens were not collected in May 2003, because of extremely low population densities present that month. The UCR site was selected for collections because all generations and life stages of *H. coagulata* were present throughout the year and because this population of *H. coagulata* was not targeted for eradication by regulatory agencies during the 3.5 yr of this study.

Homalodisca coagulata specimens were primarily collected using a beating stick to strike branches, causing adults to drop from branches into a sweep net. Specimens were selected at random from these collections. Once captured, the adults were injected with 70% ethanol into the abdomen using a microsyringe and stored in 70% ethanol until dissected. Five to 20 specimens were randomly selected from vials containing the entire collection for each sampling date and dissected in 70% ethanol. Dissections were made under a stereoscope (MZ12.5; Leica Microsystems, Melville, NY) fitted with a light source (L2, Leica Microsystems). A total of 993 females were dissected.

An ovarian rank was assigned to each dissected specimen as described by Hummel et al. (2006) (Table 1). Briefly, ovarian rank 0 females had zero oocytes visible and no corpus luteum in each ovariole. Ovarian rank 1 females had one oocyte and no corpus luteum in each ovariole. Ovarian rank 2 females had two oocytes and no corpus luteum in each ovariole. Females assigned an ovarian rank of 0, 1, or 2 were further combined into the category of previtellogenic females. Ovarian rank 3 females had two immature and one mature oocyte per ovariole. Ovarian rank 4 females had one immature, one maturing, and one mature oocyte per ovariole. Ovarian rank 5 females had one immature and one maturing oocyte per ovariole. Females assigned an ovarian rank of 3, 4, or 5 were combined into the category of vitellogenic females. Ovarian rank 6 females had two immature oocytes and a corpus luteum in each ovariole. Ovarian rank 7 females had one immature oocyte and two corpora lutea per ovariole. Females assigned an ovarian rank of 6 or 7 were combined into the category of postvitellogenic females. All sampling dates for each month were combined (Fig. 1), and the proportion of previtellogenic, vitellogenic, and postvitellogenic females was calculated and plotted by month of collection (Fig. 2).

Modeling. Months were assigned as variables according to the following criteria: $s_1(t)$ (where s denotes the month) is equal to 1 if the month is January (s_1) but equal to 0 otherwise. Variable $s_2(t)$ is equal to 1 if the month is February (s_2) but equal to 0 otherwise; and so on for the calendar year. The proportion of previtellogenic females in each month was assigned the notation $\mathrm{Pre}(t)$. The proportion of vitellogenic females in each mo was assigned the notation $\mathrm{Vit}(t)$.

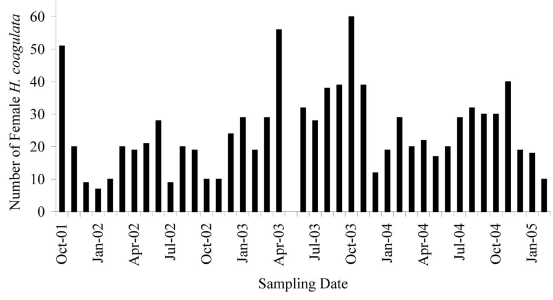

Fig. 1. Total number of female *H. coagulata* specimens collected and dissected per month from citrus at the University of California, Riverside, Agricultural Operations from October 2001 to February 2005 ($n_{total} = 993$).

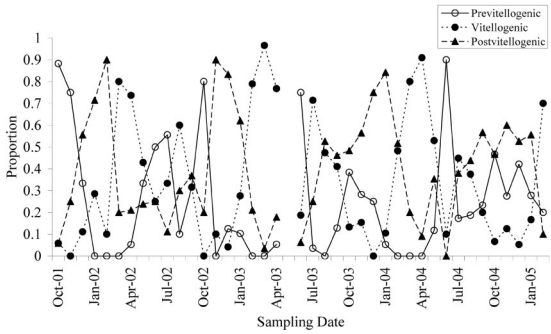

Fig. 2. Proportion of female *H. coagulata* in each ovarian rank collected and dissected per month from citrus at the University of California, Riverside Agricultural Operations, from October 2001 to February 2005. Previtellogenic females have not yet ovulated. Vitellogenic females have mature or maturing eggs in their ovarioles. Postvitellogenic females have ovulated and have a corpus luteum in their ovarioles.

The simplest time-dependent predictive modeling scheme would be to consider an autoregressive model of order p:

$$\mathrm{Y}(t) = \beta_0 + \beta_1 \mathrm{Y}(t-1) + \ldots + \beta_p \mathrm{Y}(t-p) + \varepsilon(t) \quad [1]$$

where $\varepsilon(t)$ are *iid* (O, σ) variables; $p = 4$; and Y = pre.

In our case, we needed a time-dependent model that is more general than the simple autoregressive model that considers predictor variables other than the past of $\mathrm{Y}(t)$. These other predictor variables are $\mathrm{Vit}(t-1)$, $\mathrm{Vit}(t-2)$, $\mathrm{Vit}(t-3)$, $\mathrm{Vit}(t-4)$, $s_1(t)$, $s_2(t)$, $s_3(t)$, $s_4(t)$, $s_5(t)$, $s_6(t)$, $s_7(t)$, $s_8(t)$, $s_9(t)$, $s_{10}(t)$, $s_{11}(t)$, and $s_{12}(t)$. This predictive model can be written as:

$$\begin{aligned}\mathrm{Y}(t) &= \beta_0 + \beta_1 \mathrm{Y}(t-1) + \ldots + \beta_p \mathrm{Y}(t-p) \\ &\quad + \gamma_1 \mathrm{X}(t-1) + \ldots + \gamma_q \mathrm{X}(t-q) + \alpha_1 \mathrm{Z}_1(t) \\ &\quad + \ldots + \alpha_r \mathrm{Z}_r(t) + \varepsilon(t) \quad (2) \quad [2]\end{aligned}$$

where $q = 4$; X = vit; Z = S variables.

A stepwise method was used to select the variables in the above time-series regression model. We believed that time dependence would only go back one generation and the length of a generation of *H. coagulata* is ~4 mo (Turner and Pollard 1959). Thus, the values of p and q were set equal to the maximum plausible value of 4 mo. Because the length of our data is moderate, and the model above has 20 parameters, a regular stepwise method may not be efficient. For this reason, we used the following modification. We first entered any predictor variable that potentially had even a small predictive ability. To this end, we ran a forward stepwise method with a small threshold of *F*-to-enter equal to 0.5. The following predictor variables were entered: s_1, s_2, s_3, s_4, s_6, s_9, s_{10}, s_{11}, $\mathrm{Pre}(t-1)$, $\mathrm{Pre}(t-2)$, $\mathrm{Pre}(t-3)$, $\mathrm{Vit}(t-3)$, and $\mathrm{Vit}(t-4)$. Next a regular backward stepwise method was performed with *F*-to-enter and *F*-to-delete equal to four, and the following variables were selected: s_2, s_4, s_6, and $\mathrm{Vit}(4)$. Minitab software (Version 14; Minitab, State College, PA) was used for the analysis.

Results

Seasonal Patterns. Dissections of female *H. coagulata* showed that there were two distinct peaks of previtellogenic females each year on citrus at UCR Ag Ops, with a third peak occurring in both December 2002 and December 2004 (Fig. 2). We define a peak in the proportion of previtellogenic females as the beginning of a generation. A peak in the proportion of previtellogenic females occurred in October 2001. Peaks in the proportion of previtellogenic females were subsequently observed in July, October, and December 2002, in June and October 2003, and in June, October, and December 2004. There was also a slight increase in the proportion of previtellogenic females in December 2003. We stopped sampling in February 2005.

The proportion of vitellogenic females was greatest in March and August 2002, March and July 2003, and April and July 2004. The proportion of vitellogenic females began increasing again in February 2005 when collections were terminated.

An inverse relationship between the peaks in the proportion of previtellogenic females and vitellogenic females occurred in each year (Fig. 2). In June, the proportion of vitellogenic females declined as the proportion of previtellogenic females increased. The decline was followed by a sharp increase in vitellogenic activity, presumably by females in the first adult generation. In October, vitellogenic activity decreased, as the proportion of previtellogenic females increased, marking the appearance of the second generation. Vitellogenic activity remained low during the winter, until temperatures began to increase in spring. The annual cycle was repeated beginning in February when the proportion of vitellogenic females increased.

Dissections of female *H. coagulata* indicate that the greatest proportion of postvitellogenic females occurs in December through February (Fig. 2). The proportion of postvitellogenic females began to increase in October 2001 and was greatest in February 2002. The greatest proportion of postvitellogenic females was found in December 2002 and again in January 2004. During the winter of 2004, no clear peak in the proportion of postvitellogenic females was found as it had been in the previous 3 yr, but there was an increase in the proportion of postvitellogenic females from late summer to early fall.

Our dissections showed that vitellogenic females occur at some level throughout the year in the study population of *H. coagulata.* Vitellogenic females were not collected in November 2001, but some vitellogenic females were collected in January 2002. The proportion of vitellogenic females remained between 5 and 10% during winter 2002–2003. Vitellogenic females were not collected in December 2003, but the proportion of vitellogenic females increased beginning in January 2004 and continued through the spring of 2004. The percentage of previtellogenic females remained at or above 5% during winter 2004–2005. The proportion of vitellogenic females present during

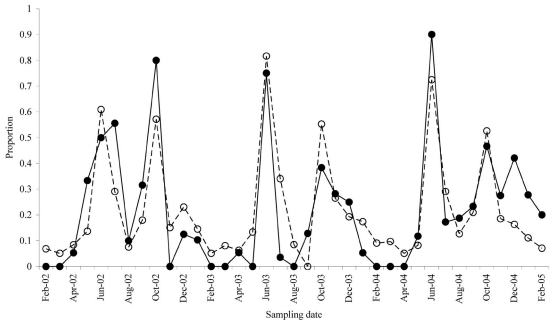

Fig. 3. Time-dependent model (equation 3) of the proportion of previtellogenic female *H. coagulata* per sample date collected from citrus at the University of California, Riverside Agricultural Operations, from February 2002 to February 2005; fitted values are indicated by the dashed line, and observed values are indicated by the solid line.

winter seemed to be related to higher minimum temperatures in a given year.

Model. Based on a fit of $\mathrm{Pre}(t)$ on $s_2(t)$, $s_4(t)$, $s_6(t)$, and $\mathrm{Vit}(t-4)$, the fitted model was:

$$\mathrm{Pre}(t) = \beta_0 + \beta_1 \mathrm{Vit}(t-4) + \beta_2 s_2(t) + \beta_3 s_4(t) + \beta_4 s_6(t) + \varepsilon(t) \quad (3) \qquad [3]$$

where, $\beta_0 = 0.0508$, $\beta_1 = 0.300$, $\beta_2 = 0.529$, $\beta_3 = 0.197$, and $\beta_4 = 0.445$. The time-series model was significant ($P < 0.001$), with an adjusted $R^2 = 0.671$ and mean square error = 0.01967 (Fig. 3). However, because there were only three data points for each s variable, this model should be viewed with caution. The most significant variables selected were $\mathrm{Vit}(t-4)$: vitellogenic activity 4 mo before time (t) ($t_{4,30} = 3.19$, $P = 0.003$); s_2: February ($t_{4,30} = 6.12$, $P < 0.001$); s_4: April ($t_{4,30} = -2.03$, $P = 0.051$); s_6: June ($t_{4,30} = 5.14$, $P < 0.001$). Of these, the variables $\mathrm{Vit}(t-4)$, s_2, and s_6 appeared to be the most important given their highly significant P values. Variable s_4 also appeared to effect peaks of previtellogenic females.

Discussion

Female dissections and assigned ovarian ranks indicate that there are two to three generations of *H. coagulata* per year in citrus groves at UCR Ag Ops in Riverside, CA. These generations are indicated by peaks of previtellogenic females in June, October, and December. Vitellogenic activity seems to be similar to that described for *H. coagulata* in Georgia (Turner and Pollard 1959) and *H. liturata* (Burks and Redak) [formerly *H. lacerta* (Fowler)] in southern California (Powers 1973). In Riverside, CA, the proportion of vitellogenic female *H. coagulata* typically increased in February, with the first peak in vitellogenic females in March. In contrast, *H. liturata* had the first peak in egg production in April (Powers 1973).

After a peak in the proportion of vitellogenic females in February, we found that *H. coagulata* adult densities decreased precipitously in Riverside, CA, in May of all 3 yr. This sudden decline in adults was also observed in Georgia (Turner and Pollard 1959) and may be explained by the death of the overwintered females shortly after ovulation. In June, the proportion of vitellogenic *H. coagulata* females declined as the proportion of previtellogenic females increased. In July, there was a sharp increase in vitellogenic activity, leading to the greatest annual proportion of vitellogenic females. Turner and Pollard (1959) and Yonce (1983) reported that first generation adults appeared in early June in Georgia, with the greatest annual adult densities occurring in late June or early July. Timmer et al. (1982) observed peak *H. coagulata* trap catch in June in Florida, whereas Yonce (1983) documented peaks in the number of *H. coagulata* in the latter part of July in South Carolina. Blua et al. (2001) reported that peak adult flight activity in Riverside, CA, occurred in July of each year from 1996 to 1999. Powers (1973) reported that the density of gravid female *H. liturata* increased from January to March and again from June to July, but that there was no distinct adult peak because of extensive generation overlap.

Second-generation adult *H. coagulata* appeared in October of all 3 yr. We found that second-generation adults of *H. coagulata* appeared when the proportion of previtellogenic females increased and the proportion of vitellogenic females decreased. Turner and Pollard (1959) reported that second-generation adults appeared in late September in Georgia and peaked in early October. Vitellogenic activity remained low until temperatures begin to increase in February of the following year. Powers (1973) found differences in female *H. liturata* fecundity between the overwintering and summer broods. Overwintering brood females laid more egg clusters than did females of the summer brood (Powers 1973). These differences in fecundity were attributed to differences in female survival, which was greater for the overwintering brood. We cannot conclude whether the first- or second-generation *H. coagulata* overwinter in Riverside, CA, but adults of both generations are capable of doing so.

In Georgia, *H. coagulata* adults survive the winter in what Turner and Pollard (1959) term an incomplete hibernation in which the insects were quiescent at cold temperatures, but were observed to feed and fly above a temperature threshold (Pollard and Kaloostian 1961). Thus, Pollard and Kaloostian (1961) concluded that *H. coagulata* survive the winter as adults but do not have a programmed reproductive diapause. Our data suggest that incomplete hibernation similar to that described by Turner and Pollard (1959) also occurs in the population of *H. coagulata* at the Riverside, CA, study site. From November to January in 2002 and 2004, the population structure consisted of ≈90% postvitellogenic females. These overwintering females may be in an induced reproductive diapause. The remaining 10% of the overwintering population is previtellogenic and may be in an incomplete hibernation. Some of our winter collections contained brown-winged females that had previtellogenic ovarioles, indicating that they were older females in a reproductive diapause (N.A.H., unpublished data). In late fall, if minimum temperatures are sufficiently

warm for reproductive activity to occur, a small peak in the proportion of previtellogenic females is observed. Although, we presume that the majority of overwintering females will not ovulate until February, a relatively small cohort may ovulate in the winter, which may explain the existence of vitellogenic females in specimens collected in January. While vitellogenic females are least abundant during the winter, reproductive activity of *H. coagulata* does not stop completely on citrus in Riverside, CA, if temperatures are sufficiently warm.

Based on reproductive development times from our dissections and that most Cicadellidae begin egg production about 7 d after eclosion (Raine 1960, Tonks 1960, Stoner and Gustin 1967, Nielson 1968, Nielson and Toles 1968), we conclude that the interval from a peak in vitellogenic females to the appearance of the next generation of young adults is between 3 and 4 mo. A time-dependent model that was generated from the analysis of our dissection data indicates that the proportion of vitellogenic females, 4 mo before time t, has the most significant effect on the proportion of previtellogenic females at time t. A lag time of 4 mo between peaks in vitellogenic females and peaks in previtellogenic females is consistent with our observation that *H. coagulata* have three generations per year in Riverside, CA, which corresponds to three peaks in the proportion of previtellogenic females. February and June seem to be the most important months in the model to predict the appearance of peaks in previtellogenic females. There is also a less significant effect of the month of April.

In this study, we characterized ovarian ranks according to Hummel et al. (2006) and found two to three generations occur each year in Riverside, CA, citrus. The occurrence of two to three generations per year is in agreement with literature on *H. coagulata* generations in Florida (Alderz 1980), Georgia (Turner and Pollard 1959), Texas (Sanderson 1905), and previous accounts in southern California (Blua et al. 1999). Thus, ovarian ranking seems to be a reliable method for characterizing seasonal patterns of *H. coagulata* reproduction. Adult peak densities typically occur in June and October, and in December, when there is a third generation. Periods of greatest ovulation occur in between March and April and again between July and August (Pilkington et al. 2005). A time-dependent model based on our 3.5-yr study of ovarian development predicts peaks in previtellogenic females based on peaks in the proportion of vitellogenic females 4 mo before time t. Clarification of the timing of reproductive events including peak periods of ovulation and mating activity can improve the timing of control activities, particularly applications of ovicides and releases of egg parasitoids.

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